

Growth and shell shape in Productacean Brachiopods

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Synopsis

The growth of strongly curved productaceans, including geniculate species, is considered both in cross section and in longitudinal section. The relationships of shell shape to dorsal valve geniculations and the pattern of spines is studied in *Overtonia fimbriata*. The importance of studying shell growth in three dimensions when making functional interpretations is stressed, and some general palaeoecological conclusions are derived.

The growth and shapes of productacean brachiopods have been described by many authors, for example Sarycheva (1949), Rudwick (1959), Williams & Rowell (1965), Brunton (1966, 1982) and Shiells (1968), but most of them considered the shell in two dimensions, and often showed only the median longitudinal section to illustrate their discussions. Other growth studies have concentrated on shell microstructures, e.g. Williams (1968, 1971), Brunton (1969) and McKinnon (1974), but seldom have growth studies presented a more three-dimensional picture by including discussion on the growth of the brachiopod in width as well as in length. In addition to considering changes in both the cross-sectional and longitudinal views of productaceans, some of the growth patterns are related to the growth of spines on one or both valves and some of these patterns may help in the interpretation of palaeoecology.

Most brachiopods grow by peripheral shell accretion. The expansion of the two valves is controlled by the directional growth of secretory epithelium, which commonly altered during ontogeny, and thus altered the shapes of individuals (Williams & Rowell 1965). However, among the productaceans there are some very curved species in which growth directions changed abruptly, leading to the development of well-differentiated ears, dorsal valve trails or marginal rims (Shiells 1968). As viewed in median section the growth of ventral valves in productaceans is planispiral, with dorsal valves assuming various strategies to maintain body size and a close fit of the commissure. Within the Productacea it is possible to identify two general shapes, with many special cases of each and a variety of intermediate forms.

The first case, exemplified by species of *Krotovia*, *Juresania*, *Echinoconchus* or *Gigantoproductus*, was probably the more primitive, having an open planoconvex to concavoconvex lateral profile in which the dorsal valve curves to meet the ventral valve close to its margin (Fig. 1). Viewed laterally, the ventral valves of these shells retain an open bowl-like shape in which the anterior margins continued to grown principally in an anterior direction. A special case within this non-geniculated group is seen in species of *Productina*, e.g. *P. margaritacea* (Phillips) and *P. pectinoides* (Phillips). In these shells the dorsal valve curves gently to the anterior margin (as seen in longitudinal section) only after having produced a sequence of lamellose trails throughout ontogeny. Prins (1968) has illustrated the numerous trails in an example of *P. pectinoides* from north-west Spain and Fig. 2 shows the trails, trapped in sediment, of *P. margaritacea* from north-west England.

The second case includes genera such as *Inflatia*, *Diaphragmus*, *Antiquatonia* or *Alitaria*, in which the dorsal valve geniculated abruptly against the ventral valve so that in adulthood the anterior regions of both valves were parallel to each other and formed a pair of trails

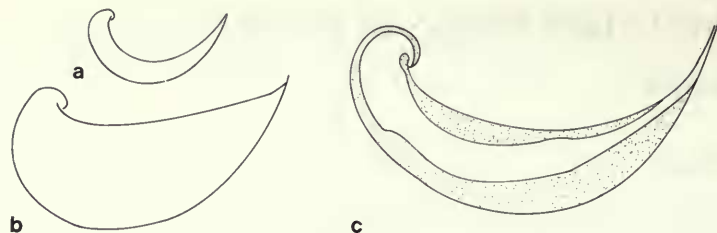


Fig. 1 Longitudinal sections of three non-geniculate productaceans, in which gently concave dorsal valves grew with the ventral valves in smooth curves. a – *Krotovia* sp.; b – *Echinoconchus* sp.; c – *Gigantoproductus* sp.



Fig. 2 *Productina margaritacea* (Phillips). The dorsal valve, exfoliated and viewed from the inner (ventral) side, showing a series of delicate lamellae extending at low angles into the surrounding limestone. The presence of these lamellae is why dorsal valve exteriors can seldom be cracked out of limestones. From the Viséan of the Clitheroe area of Lancashire. B336, $\times 1.5$.

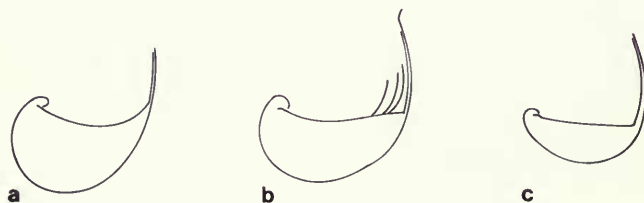


Fig. 3 Longitudinal sections of three productaceans with geniculated dorsal valves and well-developed trails. a – *Inflatia* sp.; b – *Diaphragmus* sp. in which the dorsal valve geniculated several times during growth; c – *Alitaria* sp.

(Fig. 3). In such shells the growth of the ventral valve, seen laterally, continued its expanding planispiral growth form so that its anterior margin grew increasing dorsally and may even have eventually overhung the dorsal valve.

In this discussion I use the terminology illustrated in Fig. 4, in which the term 'visceral cavity' includes the internal space occupied by the body and brachial cavities of the living animal. 'Lamellae' are surface shell ornamentations, some of which may have been trails at their time of growth at the valve margin. 'Trails' are developed only at the valve margins; they normally involve both valves and produce a narrow aperture. The term 'geniculation' is

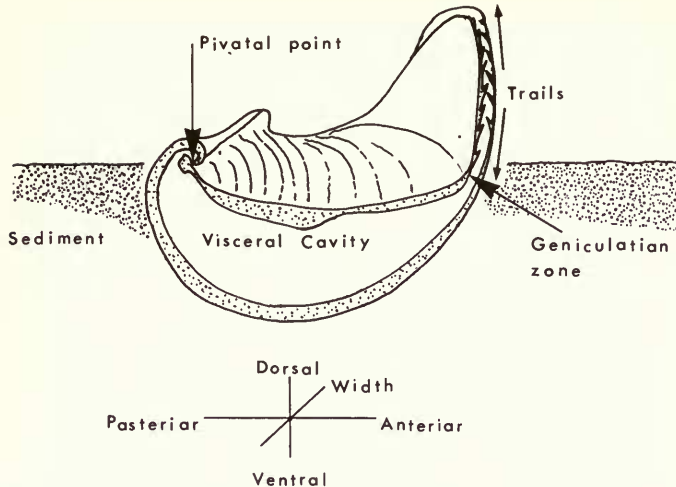


Fig. 4 Stylized longitudinal sagittal section of a productacean with a geniculated dorsal valve and well-developed trails. The pivotal 'point' is that about which the dorsal valve rotated when normally opening and closing, and also about which the valve hinged while increasing the depth of the visceral cavity.

restricted to abrupt angular changes in growth direction. Thus, other than in the growth of marginal rims or ears, where the geniculation is outwards, ventral valves in productaceans are not geniculate, but ventral valve geniculation is seen, for example, in leptaenids.

There is a problem in the increase of visceral cavity sizes in highly curved brachiopods, such as productaceans. Viewed in cross section, a brachiopod could only increase its visceral cavity width while the growing lateral margins continued to extend outwards (Fig. 5). Once the lateral margins had curved dorsally to the extent that they were parallel to each other (a full cross-sectional curve of 180°) it would then be impossible to widen the visceral cavity without a strong outward curve which, if followed by the dorsal valve, would produce a narrow trail-like rim. This type of growth is commonly seen in the posterolateral regions of productaceans in the formation of ears (Fig. 6). Ears are important morphological features for concavoconvex brachiopods such as productids or chonetids, because they provided the main posterior support for the dorsal valve (Fig. 7). Without ears the dorsal valve would have been pulled into the body cavity when the muscles contracted (see Brunton 1982). In

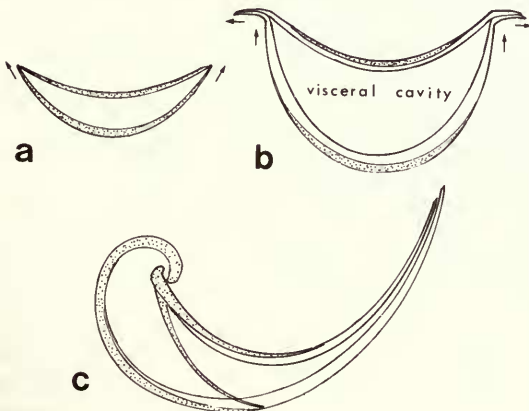
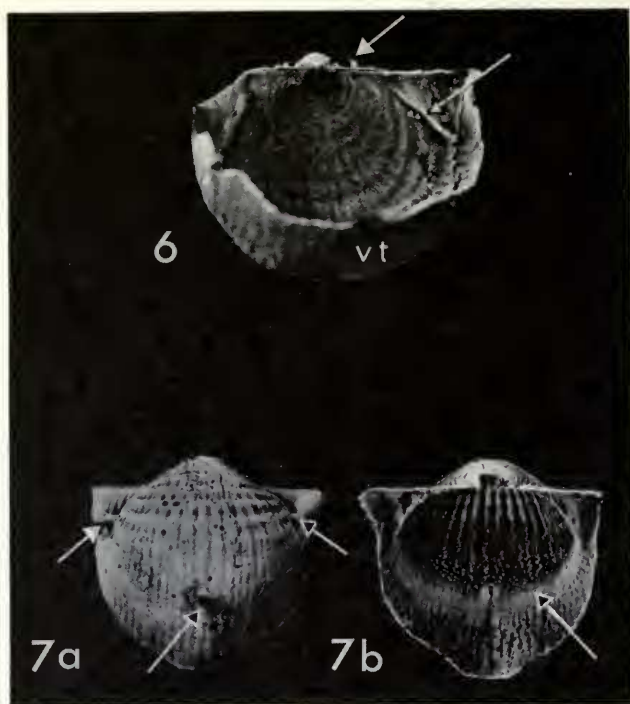


Fig. 5 Stylized cross sections of a productacean (a) when young, while growth of the valves continued to widen the visceral cavity, and (b) in adulthood, when it was impossible for the visceral cavity to increase its width. Increased width of the complete shell was achieved only by lateral geniculation of the ventral valve. (c), longitudinal section of a non-geniculated shell at the two stages of growth represented by (a) and (b).



Figs 6, 7 *Eomarginiferina trispina* Brunton, 1966, from the Viséan of Co. Fermanagh, Ireland, a species with well-developed ears formed by the lateral geniculation of part of the ventral valve margin. Fig. 6, anterodorsal view of an almost complete shell showing the clearly-defined ears providing support platforms for the dorsal valve; vt = ventral trail. The two arrows point to the stumps of juvenile clasping spines and to the dorsal valve ridge separating the visceral area from the ear. BB52890, $\times 4$. Fig. 7, a ventral valve seen externally (7a) and internally (7b), showing the ears and positions of the three major spines (arrowed on 7a) which occur close to the place where the dorsal valve met the ventral valve; this smooth zone is arrowed on 7b. BB52893, $\times 3$.

addition ears probably acted as stabilizers, preventing the posterior end of the productaceans from sinking too deeply into the sediment, and in some species they may have had a role to play in providing areas for gonadal tissues. However, the lateral growth of ears normally added significantly neither to the volume of the visceral cavity nor to its width, although they often added considerably to the maximum width of the whole shell.

The other alternative for widening the visceral cavity would be by shell resorption and redeposition. Resorption of shell material is well known in some brachiopods, such as in the loops of terebratulids or the growth of cyrtomatodont teeth. These are instances of modifications only to internal shell structures composed of secondary shell enveloped by epithelium. In no instance do we see natural resorption of the outer primary shell layer of brachiopods, other than perhaps for the unusual umbonal structure termed the 'colleplex' by Wright (1981), found in *Dictyonella* and *Isogramma*. (The increased size of the foramen of some older specimens of terebratulids should, I think, be explained entirely by shell abrasion.) The external ornamentation of brachiopods is determined by growth of the outermost primary shell layer, and had this been resorbed, to allow widening of the visceral cavity, the external ornamentation would have been destroyed, the new growth being differentiated by a discontinuity of ornament. Such breaks in ornament are only seen in specimens in which the shell has been damaged. Thus once the cross-sectional curve of the ventral valve had reached 180° , a U-shape, it became impossible to widen the internal

visceral cavity. Depth could be increased by dorsal rotation from the hinge line of the dorsal valve, provided the anterior margins could be kept together (see the discussion on *Overtonia fimbriata* below).

This growth constraint means that if different individuals of a species grew to different widths in their U-shaped cross sections, perhaps at different stages in ontogeny, the ultimate adult widths of the specimens (not including ears) also varied. Growth, as seen in longitudinal sections, may have continued, producing a longer and dorsoventrally deeper specimen. In practice one finds some productacean species, apparently all fully grown and conspecific, in which the widths vary. This is especially true of the strongly curved dictyoclostids, antiquatonias and marginiferids. For instance, in a sample of silicified *Eomarginifera derbiensis* (Muir-Wood), specimens vary from 18 mm wide across the visceral region to 28 mm wide. Similarly, a sample of *Eomarginifera setosus* (Phillips) from one locality all appear to display adult characteristics, but vary from 12 mm to 19 mm in width, measured immediately in front of the ears.

As seen in longitudinal section, productaceans grew larger during late stages in ontogeny by following the growth patterns discussed above. The result of both growth patterns produced a commissure with trails, at least in adults. In the non-geniculate species the trails were shorter and more like narrow funnels widening inwards, but some, such as *Kochiproductus*, augmented the trail effect by producing externally-directed flanges (Shiells 1968). In a functional morphological study of *Levitusia* I (1982) discussed the advantage of trails to the living brachiopod. Many productaceans were adapted by shape, spine patterns and trails to live semi-infaunally on soft substrates. In such conditions, with much of the visceral region buried in sediment, long trails would have lifted the anterior and anterolateral commissure well above the sediment and allowed for the intake of cleaner water in the median sector. The gape of productaceans was commonly small, so the incurrent would have passed between two subparallel ciliated epithelial surfaces within a few millimetres of each other. Trails are normally strongly endospinous and these probably prevented larger particles from entering the brachial cavity. The ciliated epithelium probably assisted the flow of water and was able to reverse so as to expel unwanted particles, including faeces. Trails, therefore, were advantageous to most productaceans.

Recently, Lazarev (1981) discussed the ontogeny of productids with trails and showed a *Productus* sp. in longitudinal section at various growth stages. The dorsal series of trails developed at particular stages in ontogeny (the onset of which Lazarev suggested was sexual maturity), starting when the dorsal valve first geniculated against the ventral valve, and in his example this occurred at about half the full length of the shell. Lazarev commented that it was not clear why these dorsal trails had grown, although he suggested a brooding function for spaces between the dorsal trails. However, once a dorsal valve had fully geniculated to form a commissural trail, it would have been impossible for the visceral cavity to increase in size. To do so, the dorsal valve developed instead a succession of short dorsal trails, each separated by a brief period of normal anterior valve growth which maintained the basic valve profile. Thus, rapid geniculation and growth of the trail was followed by mantle regression to the pre-geniculation position and renewed normal forward growth to maintain a good commissural fit (Fig. 8a,b). As the dorsal valve grew forwards, it rotated slightly dorsally from the hinge and this increased the depth of the visceral cavity.

A good example of the intimate relationship between growth of the valves, their trails and lamellose surfaces, and with spines, is *Overtonia fimbriata* (J. de C. Sowerby) (Fig. 9). As seen in longitudinal section, the ventral valve grew in a regularly expanding spiral curve, but at regular intervals a series of concentric ridges, called rugae, were developed (Fig. 9). The dorsal valve grew almost flat, but with a series of short lamellae virtually perpendicular to the external surface, each of which had been a marginal trail for a short period (Fig. 9c). Spines grew from both valves. On the ventral valve more or less erect spines grew from the proximal slope of each ruga and recumbent spines from the slightly lamellose distal slopes: i.e. near the base of each depression between the rugae (Fig. 9d). Dorsal valve spines grew immediately after the growth of each upstanding lamella. As the ventral valve grew,

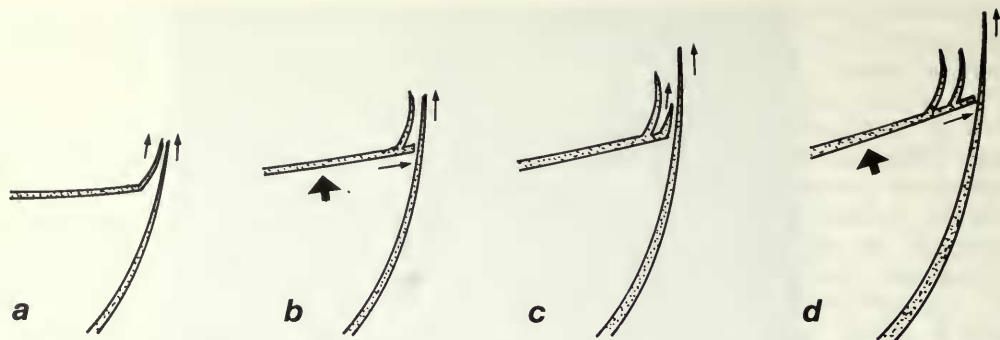


Fig. 8 Diagrammatic representation of growth at the anterior shell margin in a multi-geniculated species. (a), both valve margins growing anterodorsally. (b), dorsal valve rotating upwards anteriorly, increasing the visceral cavity depth, as its margin grows anteriorly against the ventral valve. (c), dorsal valve static, but its margin is geniculated and growing dorsally, parallel to the ventral valve. (d) as in (b).

increasing the distance between its margins and the umbo, the dorsal valve increased its length, while rotating slightly at the hinge to increase the visceral cavity depth. At the start of growth of each ventral valve concentric ruga, the dorsal valve margin grew, increasing the valve length and also budding a concentric band of spines. By the time growth had continued to the crest of the ruga, growth in the dorsal valve had altered, so that instead of expanding its dimensions it grew a short geniculated trail, as at positions A and C of Fig. 10. This maintained a close fit with the ventral valve while the distal side of the ruga grew in an arc retaining approximately the same distance from the pivotal point at the umbo. This pattern was repeated throughout growth of the shell, but with ever more closely spaced dorsal valve trails later in life, as the ventral valve ceased to add much to its straight line length from the umbo to its anterior margin. This diminution in the rate of spiral expansion also accounts for the flattening of the ridges on the ventral valve anteriorly, since less inward bend of the shell surface, at the distal side of the ruga, was necessary to allow for the non-expansion period of trail growth by the dorsal valve. In *O. fimbriata* two rows of differently orientated spines grew on each ventral ruga. The dorsal valve alternately extended its disc area, while growing a row of erect spines, and then produced the short high-angled trail (Fig. 9c). The ventral valve lamellae and recumbent spines correspond with the period of trail growth on the dorsal valve. Thus lamellae, involving mantle regression, were formed simultaneously on both valves. Had growth of the dorsal valve simply followed the margin of the ventral valve without geniculating, the disadvantages would have been both that there would have been no good commissural trail at any time during ontogeny, and also that the dorsal valve would have been strongly concave and similarly rugose, allowing no increase in the depth of the visceral cavity during growth, and producing an internal dorsal surface requiring much shell deposition to allow for the muscle and lophophore attachments.

While the North American *Fimbriaria* follows the growth pattern of *Overtonia* closely, the sparsely spinose, radially-ribbed linoproductid *Fluctuaria* from Europe had valve margins which grew together in a series of concentric ridges on both valves. However, the expansion rate of the growth curve is greater in *Fluctuaria* than in *Overtonia*, allowing the two valves to grow as they did. The ventral valve rugae of *Overtonia* may have resulted from the 'need' to grow a sequence of trails throughout life. Alternatively, or in addition, the concentric rugae may have been an adaptation to semi-infaunal burial in soft sediment; rugation is a common feature on the posterior regions of many productaceans. The continued development of spines throughout life might be taken as an indication either of deep burial in the sediment or of the spines having provided the open commissure with a wide-mesh protective grille.

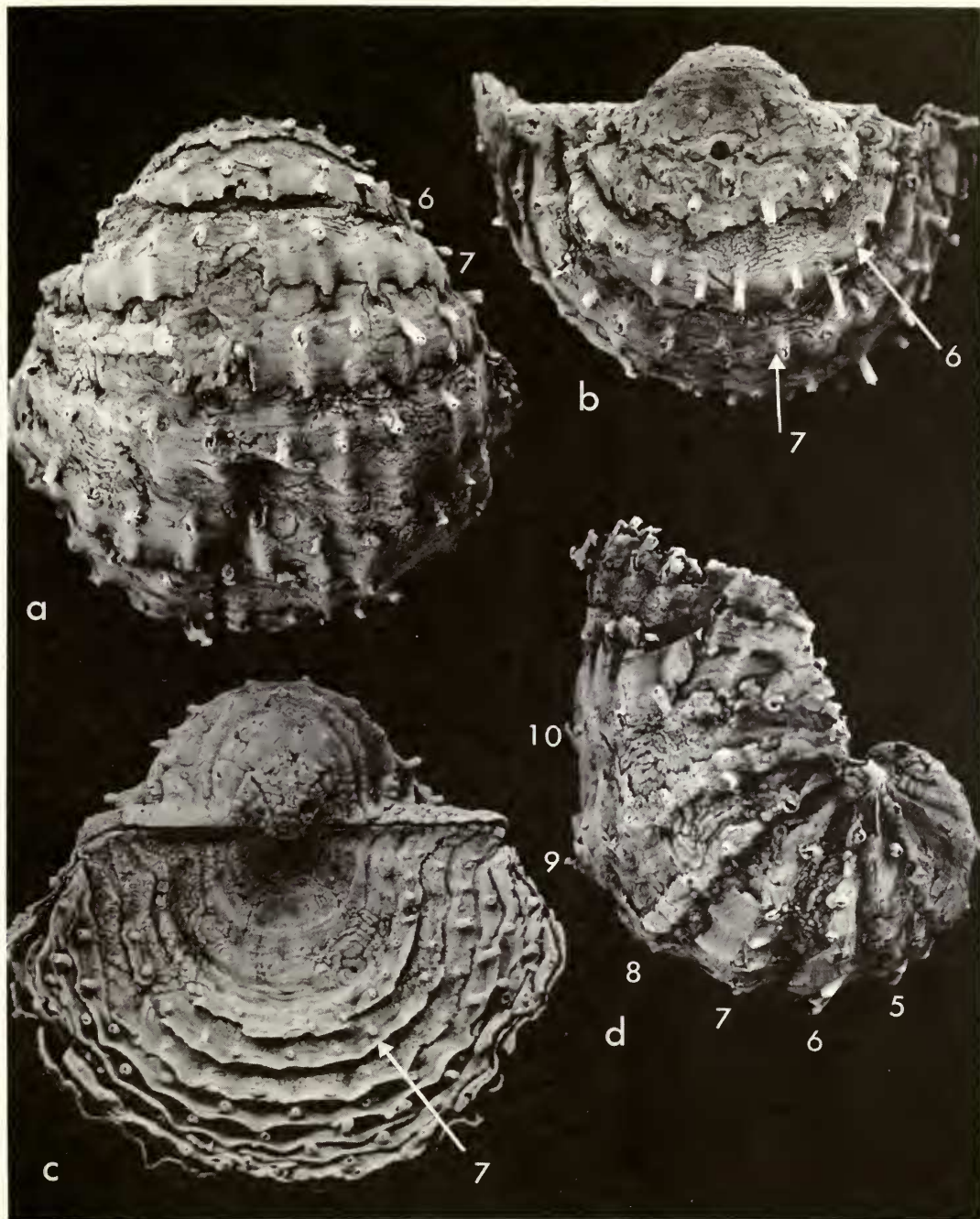


Fig. 9a-d *Overtonia fimbriata* (J. de C. Sowerby), a silicified specimen from the Lower Carboniferous, Asbian, of Co. Fermanagh, Ireland. The crests of rugae on the ventral valve have been numbered in such a way as to relate to those of Fig. 10, p. 280, but the two figures should not be taken as representations of the same specimen. The ruga numbered 7 grew at the same time as the lamella on the dorsal valve numbered 7 (Fig. 9c). The radial alignment of spines on every second row can be seen on both valves, for instance at the arrows marked 6 and 7. The recumbent lamellose spines (e.g. ruga 7 of Fig. 9a) can be seen projecting towards the gaps between the erect and recumbent spines of the next ruga. The specimen is seen in ventral view (a), posterior view (b), dorsal view (c) and lateral view (d). BB52845, $\times 4.5$.

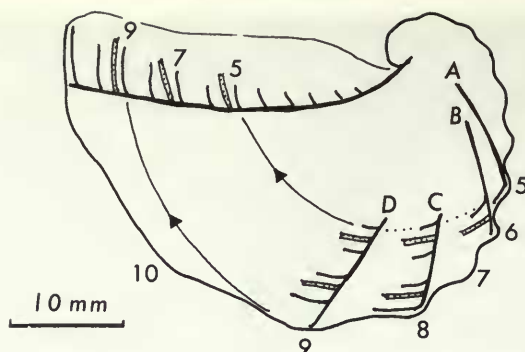


Fig. 10 Diagrammatic representation of *Overtonia fimbriata* in longitudinal section, showing the relationship of the dorsal valve, its lamellae and spines (finely stippled) with the ventral valve concentric rugae at several growth stages, A–D. For reference purposes the crests of four rugae are numbered 5, 6, 8 and 9. Dorsal valve lamellae started to grow when the valve margin was at the crests of these rugae, and the resulting lamellae (5–9) are marked. The rotations of points 5 and 9 on the dorsal valve are indicated, showing the movement from dorsal valve positions A to D, and to the adult position. Dorsal valve spines, on any one radial alignment, grew after the growth of every second lamella. Ventral valve spines (not illustrated) grew in similar alternating rows, but the two spines on a single ruga remained on the same radius so that the recumbent spines projected to the gap between spines on the next ruga anteriorly (see Fig. 9b).

The latter function may have been served by the distal recumbent spines of each ruga, which extended anteriorly beyond the valve margin.

Many productaceans, such as *Plicatifera*, most marginiferids, *Antiquatonia* and *Costiferina* grew large straight spines in distinctive patterns on their ventral valves late in life, after a period when small spines grew scattered over their more posterior regions. The large straight spines are not normally found very close to the ventral valve margins of adult shells, but some distance back, commonly in positions more or less where the dorsal valve meets or geniculates against the ventral valve (Fig. 7b, p. 276). If specimens are orientated so that a line through the umbo and the anteriormost large spines is horizontal, this probably approximates to the attitude of the specimen on or in the substrate, with the spines protruding close to the sediment surface. Before assuming its final adult position, the shell must have retained a favourable position during growth by a rotational sinking of the anterior part of the shell relative to the umbo. Without this rotational movement the shell would have grown with its adult trail overhanging the umbo, or even with its trail and commissure resting on the sediment posteriorly – a position in which survival would not have been possible.

Species having valves more or less covered by spines tend to have finer spines, commonly extending to the valve margins: such are productellids, overtoniids, echinoconchids and some buxtoniids. Some representatives of these taxa probably used their spines to entangle in clusters, but many do not have strong curvature with long trails, and these probably lived semi-infaunally with much of the shell below the surface of a soft sediment. Species with a proliferation of fine spines on both valves extending right to the margins probably gained protection at the gape against small organisms entering the shell, since the spines would have partially interdigitated across the commissure.

Much of the proliferation of productaceans during the Carboniferous period was probably in response to the development of strategies to cope with living on soft bottoms. By contrast, many strophalosiaceans and aulostegaceans are characterized by morphologies showing adaptations to life on hard surfaces, commonly in varied reef environments. Cementation early in life or throughout life, and spines capable of entangling or fixing to hard surfaces or

of growing around hard objects, are yet other modes of life. While strophalosiaceans had their origins in the early Devonian and continued through the Carboniferous in the relatively rare reef environments, it was in the Permian, at a time when hardgrounds and reefs were commoner, that strophalosiaceans and aulostegaceans flourished most abundantly. The taxonomic relationships of these groups might be clarified by treating aulostegaceans as productaceans specialized to life on hard substrates.

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